

Interactions between ericaceous plants and their competitors with special reference to soil toxicity

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Summary The major 'free' organic acids of *Calluna* heathland soil have been isolated, identified and are shown to consist of a mixture of phenolic (aromatic) and hydroxyalkanoic (aliphatic) compounds. Yields of both classes of compound follow a seasonal pattern, maximum quantities being found in summer months when they reach levels considerably higher than those found in non-heathland soils. Seedling bioassays demonstrate that several of the individual acids are highly phytotoxic at low concentration, and that a mixture of the acids at a concentration representative of that found in mid summer produces total inhibition of grass seedling root growth at low pH. High H^+ ion concentration, by itself, produces major phytotoxic effects below pH 4.0 if the base status of solutions is low.

It is concluded that the toxicity of heathland soil arises as a result of a syndrome of interactions between high organic acid content, low pH and base status, and that these interactions produce phytotoxicity sufficient to exclude or debilitate most would-be competitors in the heathland environment. The success of ericaceous plants in these hostile circumstances is attributed to their mycorrhizal associations which confer resistance to the soil toxins and provide access to complexed organic nutrients.

INTRODUCTION

Since large areas of the northern hemisphere support almost pure stands of ericaceous plants it is of great ecological interest to improve our understanding of the nature of the relationship between these plants and their competitors be they trees or herbaceous species. The topic is also of applied significance since attempts to increase the productivity of heathland areas by conversion to agriculture or forestry have been widely made. Management of heathland vegetation or more successful establishment of an introduced crop can only be obtained through a better knowledge of the fundamental interactions within the heathland ecosystem. Methods for the control of major ericaceous species such as *Calluna vulgaris* and *Rhododendron ponticum* are known and were fully described at the previous conference (McIntosh, 1980; Robinson, 1980; Brosnan, 1980) but despite some experimental analysis (Jalal & Read, 1983a, b) we still know too little about the factors which enable ericaceous plants to successfully exclude or 'check' competitors in many circumstances.

It has been shown (Read & Jalal 1980; Read 1983) that the success of ericaceous plants in nutrient poor habitats can be partly attributed to specialized mechanisms involving absorption of otherwise unavailable compounds by mycorrhizal fungi. There remains the possibility that soil

Fig. 2. Root growth of seedlings of *Agrostis tenuis* in bioassays with individual phenolic acids at a concentration of 0.3 mM and at a range of pH levels. Vertical bars indicated 95% confidence limits.

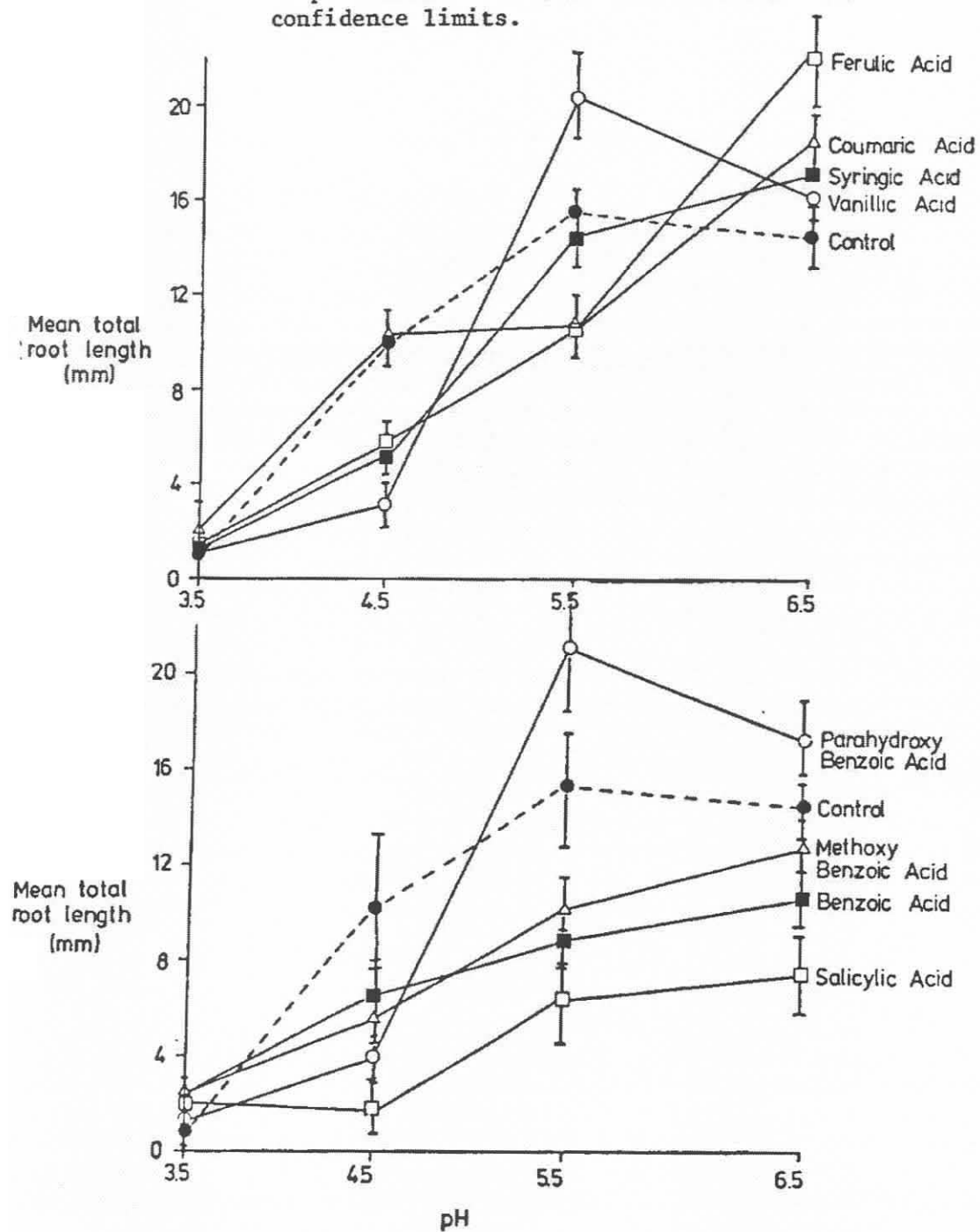


Fig. 3. As in Fig. 2 but using individual aliphatic acids.

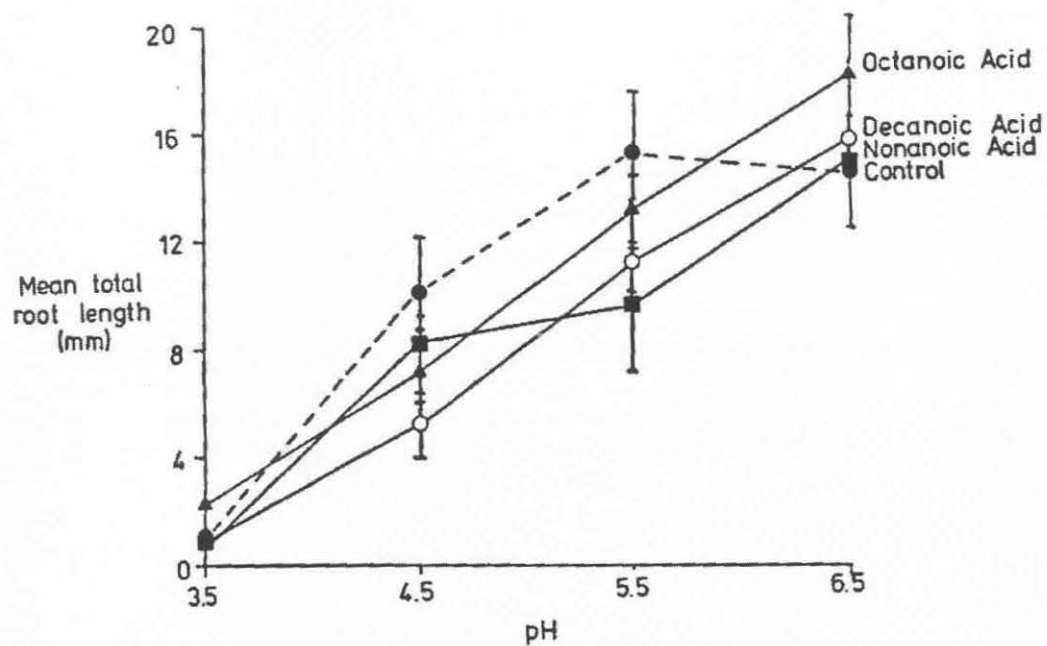


Fig. 4. As in Fig. 2 but using a mixture of all identified compounds at the typical summer concentration (0.265 mM) shown in Table 1.

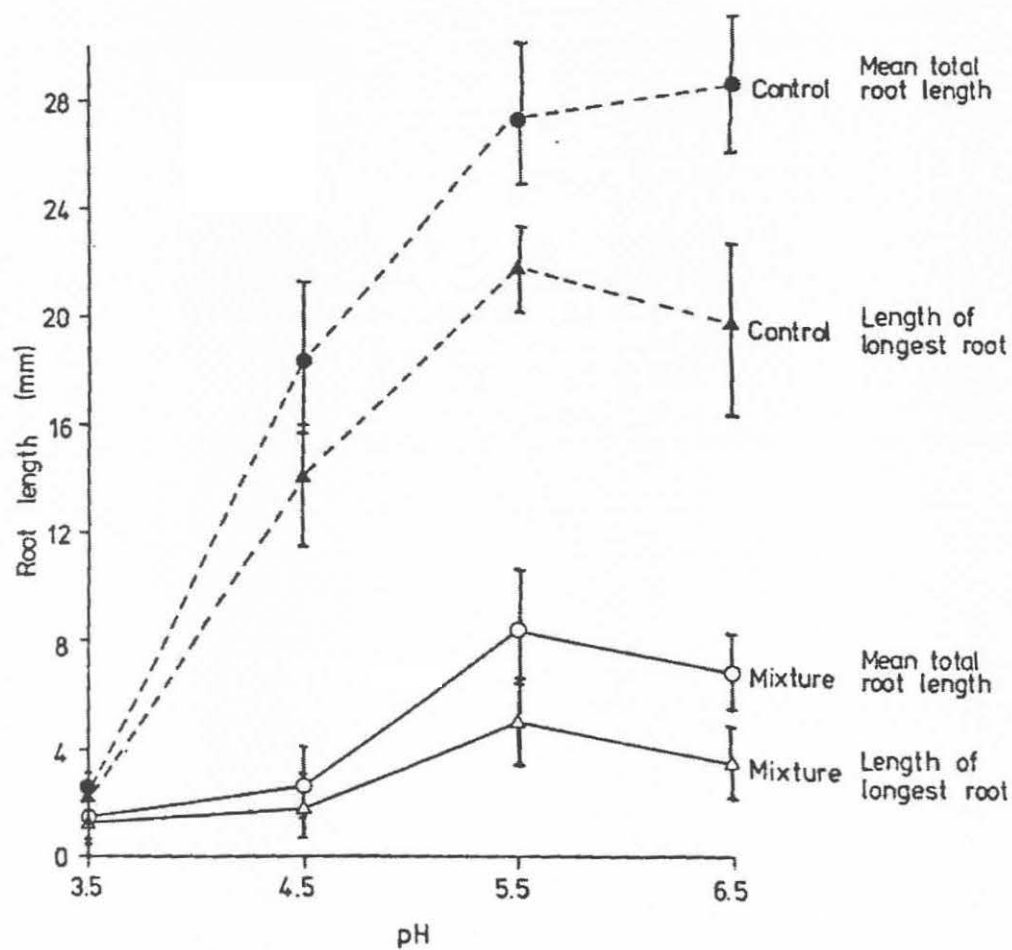


Fig. 5A & B. Concentrations of aromatic and aliphatic acids through the year in Calluna Oh (5A) and Ah (5B) horizons.

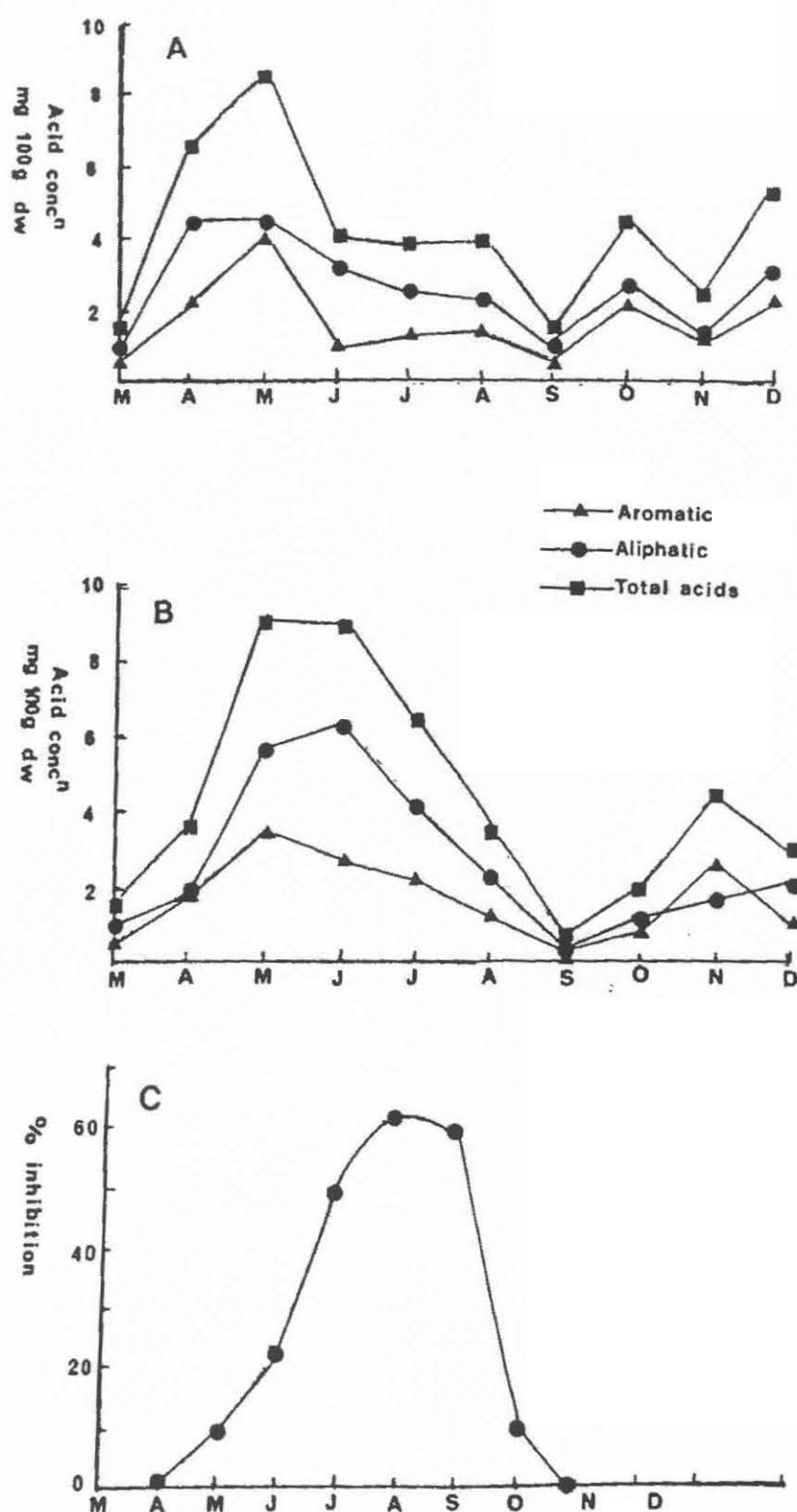


Fig. 5C. Inhibitory effects of extracts of Calluna soil when applied to tomato roots by Robinson (1971). Seasonal production of organic acids is seen to follow quite closely the demonstrated inhibitory effect of extracts. Data of Fig. 5C are reproduced by kind permission of Blackwell Scientific Publications.

Fig. 6. DIAGRAMMATIC REPRESENTATION OF THE CALLUNA
TOXICITY SYNDROME

PLANTS TOLERATE LOW pH,
LOW AVAILABLE SOIL NUTRIENT
STATUS AND HIGH METAL
CONCENTRATIONS



SPECIALISED MYCORRHIZAL ROOT
SYSTEM EFFICIENTLY SCAVENGES
FOR NUTRIENTS AND PROVIDES
RESISTANCE TO METAL TOXICITY



PRODUCTION OF LITTER
WITH HIGH PHENOL AND
LIPID CONTENT AND
LOW PROTEIN AND BASE
STATUS



DEPLETION OF SOIL BASES NOTABLY
AMMONIUM AND CALCIUM AND
ENHANCEMENT OF H⁺ ION
CONCENTRATION



ACIDIFIED MOR-HUMUS CONTAINING
HIGH CONCENTRATION OF PHYTO AND
FUNGI-TOXIC ORGANIC ACIDS
PRODUCED BY MICROBIAL DECOMPOSITION
OF TISSUE RESIDUES. THESE PRESENT IN
HIGHLY TOXIC UNDISSOCIATED STATE AT
LOW pH.



ACCELERATED LEACHING AND FURTHER
ACIDIFICATION

toxicity contributes to the exclusion of plants from heathland environments. Calluna is known to acidify the soil in which it grows (Grubb *et al.* 1969; Grubb & Suter 1971) and, as is the case in other ericaceous plants, its tissue contains high concentration of potentially toxic secondary metabolites notably phenolic acids (Jalal *et al.* 1982) and lipids (Tschager *et al.* 1982). These compounds eventually reach the soil under the ericaceous plants where they are metabolised by micro-organisms. There is no doubt that such soils can be highly toxic since radicle extension of grass seedlings placed onto them is often completely inhibited (Roff 1964; Read & Jalal 1980). A comprehensive analysis of the organic acid composition of heathland soil has been recently reported (Jalal & Read 1983a, b) and seedling bioassays using the identified compounds have now been carried out in order to determine the toxicity of the acids identified. We examine, here, some of the relationships between hydrogen ion concentration (pH), organic acid composition, and growth of seedlings.

MATERIALS AND METHODS

Soil analysis Soil was collected from a Calluna dominated heathland at Cropton Forest, North Yorkshire (NGR 764969). A few plants of some other ericaceous genera notably Vaccinium and Erica were associated with the Calluna but non-ericaceous species were generally absent except in disturbed sites.

Cores were taken by sinking 10 cm diameter steel tubes into the soil to a depth of 30 cm. Tubes containing the soil were transported immediately to the laboratory where they were stored overnight at 5°C. The cores were extracted from the tubes and sectioned to provide the horizons required for analysis. The surface litter (L) was discarded and two sub-surface horizons were selected and separated. These were a semi-fibrous dark brown Oh (= AoF) layer of approximately 10 cm depth and a fully humified black Ah layer of 20 cm or more in depth. This peaty material was typical of that frequently referred to as Calluna 'raw humus'.

The Oh layer was carefully sorted to remove large woody material and the Ah layer was passed through a 2.5 mm sieve. Small subsamples of each horizon were taken at this stage for analysis of total organic matter, carbon, nitrogen and water contents, and for pH determination.

Water content was determined by drying soil overnight at 80°C and pH was measured in a 2:1 v/v distilled water-soil mixture.

Extraction of organic acids An alkaline ethanol extractant similar to that described by Wang *et al.* (1967a) was employed. This extractant is strong enough to free adsorbed organic acid anions but too weak to cause hydrolysis of most organic compounds. Details of the extraction procedure are presented in Jalal and Read (1983a).

Gas chromatography-mass spectrometry Combined GLC-MS analyses of the tri-methylsilylated organic acids were carried out. Compounds were identified by analysis of their mass-fragmentation patterns.

Concentrations of the individual organic acids were calculated from the peak areas of the GLC traces. Those of the phenolic acids were obtained by comparison with standards of known concentration and those of the fatty acids were calculated using vanillic acid as the standard. Total monthly concentrations of aromatic and of aliphatic acids were obtained by summing the individual figures and, by adding the concentrations of

aromatic and aliphatic acids for each month, the figure for the total acids was obtained. When molar quantities are presented rather than weight of acid, these were calculated on the assumption of a soil water content of 70% which prevailed for much of the year. Volatile fatty acids were excluded by the extraction procedure as were fatty acids of carbon lengths above 12.

Seedling bioassays In order to determine the phytotoxicity of the organic acids, bioassays were carried out in which newly germinated seedlings were exposed for specific time periods either to the individual organic acids identified in the soil extracts or to a mixture of these acids made up to provide a concentration equivalent to that determined in a representative month in extracts of fresh soil. The individual acids were dissolved in distilled water at a concentration of 0.3 mM which is comparable with the total acid concentration of summer months. Mixtures were made up in the same way but using quantities of each acid equivalent to that recorded in the month of June. The composition and concentration in the final solution is shown in Table 1. Some of the fatty acids were not fully soluble in water in which case they were dissolved first in equimolar concentrations of KOH. The effect of pH on the phytotoxicity of the compounds was determined by running each bioassay over the ecologically important pH range 3.5-6.5. pH was adjusted to the required level by addition of H₂SO₄ or KOH. Because the buffering capacity of the solutions was so low the quantities of sulphate or potassium ions added to any solution were negligible.

Table 1. Constitution of the organic acid mixture used in the seedling bioassay experiments. The final concentrations of the individual compounds are the same as those obtained in extracts of Calluna soil (Ah horizon) in June.

Acid	Molecular weight	Concentration in Solution mg l ⁻¹	Molarity in mixture mM l ⁻¹
Benzoic	122	4	0.03
Methoxybenzoic	152	3	0.02
Salicylic	138	4	0.02
p-hydroxybenzoic	136	2	0.015
Vanillic	168	3	0.02
Syringic	198	1	0.005
Coumaric	164	0.3	0.002
Ferulic	194	0.1	0.005
Octanoic (caprylic)	144	9	0.06
Decanoic (capric)	172	14	0.08
Nonanoic	158	1.8	0.01
<hr/>			
Mean MW	159	Total Conc ⁿ 42.2	Total Molarity (mM) 0.265

Agrostis tenuis, a grass of heathland environments, was chosen as the major test species because of its ecological importance as a potential competitor in vegetation dominated by ericaceous plants and because its yields rapid and consistent seed germination.

1. Benzoic acid
2. p-Methoxybenzoic
3. U-3
(unidentified)
4. U-4
(unidentified)
5. 3-Hydroxyoctanoic acid
6. O-Hydroxybenzoic acid
(salicylic acid)
7. p-Hydroxybenzoic acid
8. 8-Hydroxyoctanoic
9. 3-Hydroxydecanoic acid
10. 8-Hydroxynonanoic acid
11. 8-Ethoxydecanoic
12. Vanillic acid
13. 8-Hydroxydecanoic acid
14. Syringic acid
15. p-Coumaric acid
16. Ferulic acid

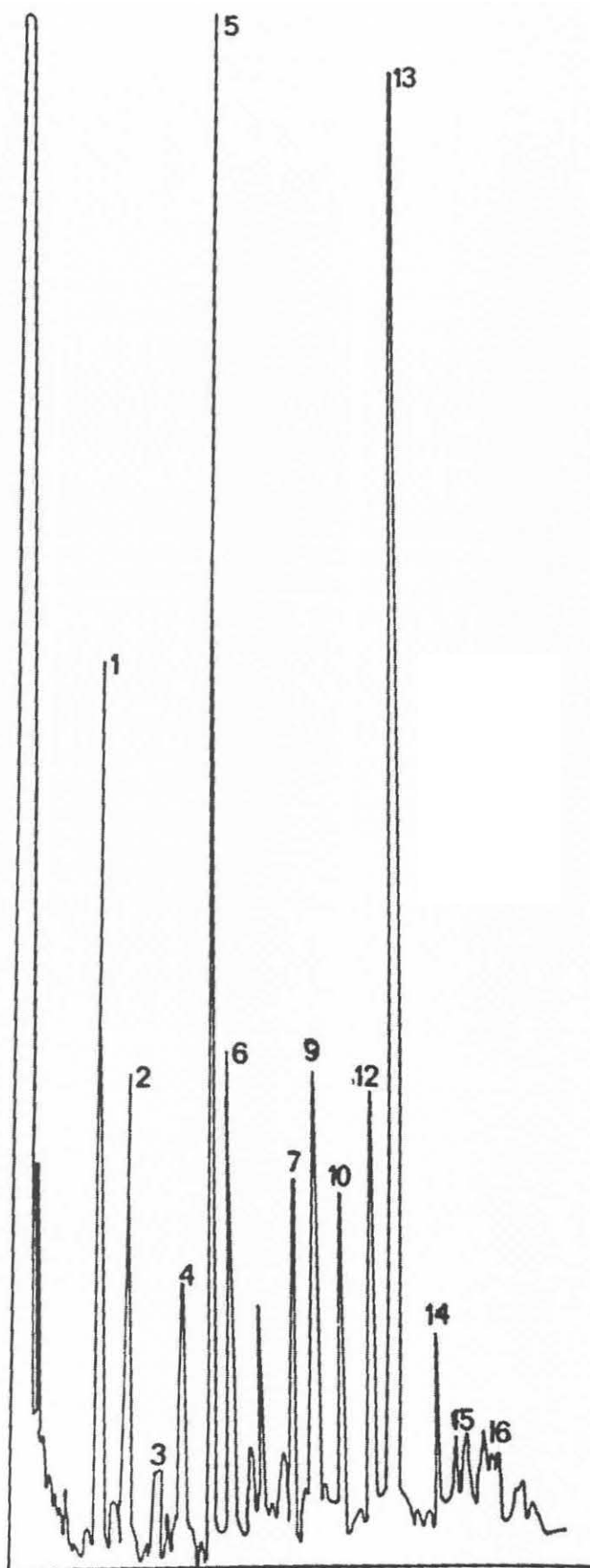


Fig. 1. Typical gas-chromatogram of organic acids obtained from Calluna Ah horizon in summer. Names of compounds giving rise to each numbered peak are listed.

RESULTS

A typical GLC trace obtained from the Calluna Ah horizon is shown in Fig. 1. The mass spectra, which are described in detail elsewhere (Jalal & Read 1983a), revealed the presence of two major classes of compound one of an aromatic nature, mostly made up of phenolic acids, and the other of an aliphatic type made up of fatty (hydroxyalkanoic) acids of short carbon chain length (Fig.1). Of the phenolic acids o-hydroxybenzoic (salicylic), p-methoxybenzoic and benzoic acid appear not to have been observed previously in unhydrolysed soil extracts. The detection of a range of hydroxyalkanoic acids was of particular interest not only because these compounds have also not been previously detected in 'free' form, but because they were identified in early seedling bioassays as being strongly phytotoxic (Prill et al 1949, van Overbeek & Blondeau 1954). Of the individual fatty acids 8-hydroxydecanoic (capric) was the major compound present in the traces of most months.

When the weights of the individual aromatic and aliphatic acids obtained each month were added together, a distinct pattern of acid production was revealed (Fig. 5a,b) a maximum yield of both classes of compound being obtained in the summer months.

Soil pH and water content varied little through the year the former being in the area of 3.5, the latter being in the range 70-80%.

Seedling bioassays a. Effects of individual compounds In all seedling bioassays a strong interaction between pH and effects of the acids is revealed (Figs. 2 & 3). Radicle growth is almost completely eliminated in all treatments, including the acidified water control, at pH 3.5. This demonstrates a sensitivity, at least at low nutrient concentration, to hydrogen ion concentrations alone. At pH 4.5, however, root growth is significantly lower than that in the control in all compounds tested with the exception of coumaric acid. At this pH the level of inhibition by salicylic and p-hydroxybenzoic acid is not significantly different from that at pH 3.5 (Fig. 2). Decanoic acid is the most toxic of the aliphatic compounds at pH 4.5, producing significantly more inhibition than the other two fatty acids tested (Fig. 3). It is however less toxic than most of the phenolic acids. At the higher pH levels differences between treatment cease, for the most part, to be significant. This is partly because of the greater variability in performance of seedling root systems as growth rates increase. The only compounds to produce a significant inhibition of root elongation relative to controls at pH 5.5 are salicylic, benzoic and methoxybenzoic acids. Significant increases of yield relative to the controls are obtained at this pH in p-hydroxybenzoic and vanillic acid. At the highest pH examined most of the root lengths are higher in the solution containing test compounds though not significantly so. Only salicylic acid produces a significantly greater inhibition than the control at pH 6.5.

b. Effects of mixtures of compounds Exposure of seedlings to mixtures of acids at a final total concentration of 0.265 mM gave highly significant reductions of both mean total root length and longest root compared to the controls at every pH level except 3.5 (Fig. 4). At this pH root growth of seedlings in both mixture and control treatments were almost completely inhibited. Root growth in the mixtures was again virtually eliminated at pH 4.5 while that of the controls showed a greater than seven-fold increase. Toxicity of the mixture is somewhat less at pH 5.5 but root length is still very significantly inhibited relative to that of the controls. As in the case of assays employing single compounds, therefore, it is possible to observe two separate inhibitory effects, one

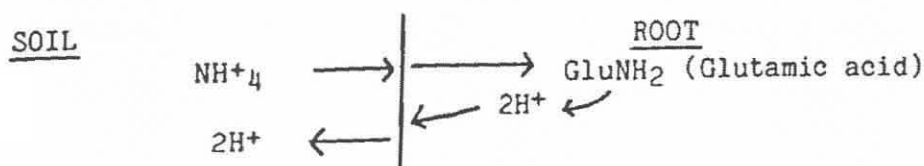
attributable to hydrogen ion concentration alone, and the other to the organic acids, this in turn being influenced by acidity. Since the inhibition of root growth at any pH level is greater with the mixture than in the case of most of the single compounds at a similar concentration it seems likely that some synergism between compounds leads to increased phytotoxicity when the acids are in solution together.

DISCUSSION

The raw humus derived from ericaceous plant litter forms a colloidal matrix of great physico-chemical complexity. It has, however, some major distinguishing characteristics each of which has now been shown to be important either by itself, or in combination, in determining the responses of introduced plant species. For convenience these factors can first be considered individually.

- They are
1. Low soil pH
 2. High organic acid content
 3. Low nutrient status

1. Low Soil pH. Calluna and Rhododendron dominated soils frequently have a pH in the range 3-4 and there is good evidence that these species acidify the soils on which they grow. The seedling bioassays reported here show clearly that such hydrogen ion concentrations can, by themselves, be inhibitory to root extension, and it is evident that this factor must always be taken into account when assessing phytotoxicity of heathland soil. It has been known since early studies of Arnon & Johnson (1942) that pH levels below 4.0 produce strongly inhibitory effects upon plant root systems but most such assays have been carried out with agricultural or horticultural crop species and so have been of relatively little ecological relevance. We now observe that similar inhibitory effects of hydrogen ion concentrations are found in species such as Agrostis tenuis the natural pH range of which has been shown (Grime & Lloyd 1973) to overlap that of ericaceous species, but to be sharply curtailed at the top end of the ericaceous range. In view of the importance of pH in this range it is necessary to consider whether the acidification arises directly as a result of the nutrient exchanges occurring at the surfaces of living roots or whether it arises indirectly as a result of the conversion of polymeric 'organic' molecules of dead ericaceous tissues to smaller anionic molecules of greater potential toxicity. Laboratory studies indicate that both factors are involved though they operate on different time scales. When grown intensively in pure sand with mineral nutrient solution at pH 4.5, Calluna and Rhododendron acidify the medium over the relatively short period of eight weeks to a figure below 4.0, and over a subsequent two month period the level is reduced further to 3.5 (Read et al in preparation). Since litter is not produced in this period this acidification must be attributable to ionic exchanges involving living roots. The most likely cause of this is absorption of cations, of which ammonium is quantitatively the most important both in the nutrient solution and in soil. It is known that NH_4 uptake takes place with compensatory extrusion of hydrogen ions and that this leads to acidification of the rhizosphere (Raven & Smith, 1976). We have:-



Analyses of sand extracts suggest that organic acids are relatively unimportant in this process so that acidification must arise primarily as a result of absorption of bases. As indicated below, (Fig. 6) initiation of acidification in this manner leads to a downward spiral of events in which the capacity to retain bases is reduced. The effect of this acidification is to produce inhibition of root growth of Agrostis tenuis, comparable with that obtained in solution bioassays or soil.

In the field, acidification is a slower process as would be expected in view of the higher buffering capacity of the soil system. Even in these circumstances, however, the acidification caused by ericaceous plants can be rapid. Sleigh (1956) reported a reduction of 0.4 units in 8 years in soil with the already low pH of 4.3, and Grubb *et al.* (1969) found rates in excess of 1 pH unit in a decade (pH 5.5 - 4.0) in both cases under Calluna. In view of the very marked effect of H⁺ ion concentration on seedling root extension at pH below 4.0 this acidification is also likely to be a factor of major importance in limiting growth of non-ericaceous plants in heathland soil. Whereas the acidification of sand was attributable largely to cation-anion exchange, in soil the important additional factor to be considered is litter quality and quantity. Plants of base poor environments like Calluna, accumulate high concentrations of organic acids, notably phenolics, which represent in excess of 28% of shoot dry weight (Jalal *et al.* 1982). This, together with the low base status, yields extremely acidic litter the pH of which is normally in the range 3.4-3.8. On humification such material will produce a rooting medium of even lower pH.

The effects of acidity on plant cells have been examined by physiologists using detached (Marschner *et al.* 1966; Jackson & Taylor 1970) or entire (Lee 1977) cereal seedlings. The major effect is upon the permeability of the cell membrane which increases markedly at pH below 4.5 leading to loss of cellular constituents, in particular of potassium, and low molecular weight organic compounds. This loss leads rapidly to structural damage and eventually to cell death. Failure of a seedling radicle to penetrate such acidic environments is not surprising since extension will involve progressively greater contact between plasmalemma and the injurious factor and hence proportionally greater loss of tissue contents.

2. Organic acids It has been known since some of the earliest seedling bioassays that organic acids can be toxic to plant roots. The aromatic acids in particular the phenolic acids have been most widely reported to have phytotoxic properties (Wang *et al.* 1967b; Glass 1976). In view of the extremely high concentration of phenolic materials in Calluna tissues it is hardly surprising that extracts of soil derived from these tissues yield high levels of the acids derived from polyphenolic sources. These acids have previously been implicated as the cause of phytotoxicity in soils dominated by ericaceous plants (Chou & Muller 1972; Carballieri 1980). Some of the phenolics shown in the present bioassays to be among the most toxic, like benzoic and salicylic acid have not been previously detected, probably because previous investigators have used paper or thin-layer chromatographic rather than, GLC procedures for separation of compounds. The greater toxicity of the o-hydroxy benzoic (salicylic) moiety has been previously demonstrated in cereal seedling bioassays (Prill *et al.*) and the records of its presence as the phenolic acid extracted in highest quantity (Jalal & Read, 1983b) indicates that it is a compound which may be of great ecological importance.

Hydroxyalkanoic acids were the other major compounds identified in heathland soil extracts (Jalal & Read, 1983a). As in the case of the phenolic acids the presence of these compounds in soil derived from ericaceous plants is not surprising since their lipid parent materials are, together with the phenolic acids, the major storage products of ericaceous plants (Tschager *et al.* 1982). These compounds are known to be produced by soil fungi as by-products of the β -oxidation of the longer chain (C16-C18) fats synthesized and stored in ericaceous plant tissues. As in the case of phenolic acids, past failure to detect the presence of the hydroxy-alkanoic acids in extracts was probably due to methodological limitations of which the most important here was the use of extractants and spray reagents specific only to phenolic compounds. It is now clear that these fatty acids are present in heathland soils in even greater quantities than the phenolics. In soil they are probably held by loose hydrogen bonding to components of the organic matter. The strength of this bonding in nature must be seen in dynamic terms. The affinity of the lipophilic alkyl chains for the organic matter may be sufficiently strong to hold the acid under most circumstances prevailing in the raw humus but if compounds of greater lipid affinity enter the environment the equilibrium of the system will be moved so that the alkanoate forms a new bonding relationship with the introduced compound. This shift can be achieved either by a solution such as the alkaline ethanol used in the extraction, which raises the pH of the environment and so causes ionization of the acceptor sites on the organic matter or, more importantly in nature, may arise when the strongly lipophilic plasma membrane of a living cell approaches the adsorption site. Studies in a range of biological disciplines have shown that the levels of toxicity exhibited by compounds in assays with living cells is closely correlated with the affinity of the compounds for lipids (Van Overbeek & Blondeau, 1954 Levitan & Barker 1972, Lee 1977). A scale based upon the solubility of the compound in octanol (the so called P-octanol index) has been derived showing a direct positive relationship between the level of octanol solubility and toxicity of a compound in bioassays. The fatty acids isolated from heathland soil and found in the bioassays to have high phytotoxicity at very low concentrations have high P octanol levels. The relationship extends even to the aromatic moieties where the most toxic of the phenolic acids, salicylic, has the highest P octanol level (Levitan & Barker, 1972).

We can therefore envisage that the compounds of high P octanol characteristic are readily miscible in the phospho-lipid membrane of the root cortical cell and that their high lipophilicity leads even those which were originally H-bonded to soil organic matter to become associated with these membranes. The result, well documented with both detached and entire roots of a range of plants is to cause the largely irreversible leakage of cellular components described earlier.

The bioassay results with perhaps the greatest direct ecological relevance are those obtained using mixtures of the compounds. It is evident that these compounds cause considerable inhibition at the concentrations experienced in summer months, though a strong interaction with pH, is observed. The seasonal periodicity of production of these compounds may be of importance since maximum yield of organic acids coincides with climatic conditions most suitable for plant growth. It is interesting to note also that the patterns of production of organic acids coincides almost exactly with the pattern of toxicity of water extracts of *Calluna* raw humus observed by Robinson (1971) using a different assay method (Fig. 5c). Though we have shown (Jalal & Read 1983a) that the compounds are not, as Robinson believed, present as free entities in water extracts they would be present in bound form in association with the water

soluble carboxylic acid polymers (previously termed fulvic acids) the yield of which is also maximal in the summer months (Jalal & Read 1983b) and their effects would be manifested through their lipophilic affinities as described above.

3. Soil Nutrient Status Soils under ericaceous plants are characteristically nutrient poor both because major nutrients such as nitrogen are precipitated with phenols in organic complexes which are resistant to decomposition, and because they are depleted of bases. One of the reasons for the success of ericaceous plants is the efficiency with which soil exploitation is achieved (Read 1983). The density of the hair root system and the effectiveness of the mycorrhizal association provides both access to otherwise unavailable organic sources of nutrients (Stribley & Read 1980) and exclusion of potentially toxic heavy metals (Bradley et al 1982). There is now good evidence that while efficiently exploiting the soil environment plants like Calluna are responsible for depletion of its base status. Grubb and Suter (1971) demonstrated a very pronounced fall in base saturation under Calluna most of which would be accounted for in terms of loss of calcium. Some of this calcium loss is undoubtedly a result of leaching processes but it is of interest that mycorrhizal infection has recently been shown to provide effective enhancement of Ca^{++} uptake in Vaccinium (Powell 1982) and Calluna (Burt unpublished). This suggests that mycorrhizal infection of roots provides a greater capability to compete for limited supplies of bases and this may in turn be a factor in the exclusion of non-ericaceous plants. Low base status and in particular a deficiency of Ca ions in the bathing medium, is well known to be a factor leading to loss of membrane integrity and leakage of ions from roots (Marschner et al 1966).

Interactions between ericaceous plants, the soils formed under them and competitors. The factors discussed above interact to produce what can best be described as a toxicity 'syndrome' which is summarised diagrammatically in Fig. 6. Ericaceous plants, with their characteristic mycorrhizal associations, are highly specialized to tolerate the adverse soil conditions which they themselves produce. Those would-be competitors, on the other hand, be they trees or herbs, which lack these specializations can flourish only when soil conditions are drastically ameliorated.

ACKNOWLEDGEMENTS

I thank Dr M A F Jalal and Mr R Bradley for skilled assistance with the analytical work and the NERC and the Forestry Commission for financial assistance.

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